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A New Species of the Baltic Amber Bee Genus *Electrapis* (Hymenoptera: Apidae)

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Abstract.—***Electrapis stilbonota***, a new species of fossil bee is described and figured from two female specimens preserved in a single piece of Eocene Baltic amber. The species is assigned to a new subgenus, ***Melikertes*** n. subg., characterized by the sparse hairs of the scutellum, outwardly curved scape, few distal hamuli, absence of hind tibial spurs, tear-drop shaped tegula, and absence of setal bands on the apices of the metasomal terga. The specimens of *E. stilbonota* are morphologically workers and were presumably from a highly eusocial colony. The classification of *Electrapis* among apines is briefly discussed, and the subtribe Electrapina proposed to accommodate the genus. The proposal that *Electrapis* and its presumed sister, *Apis*, coexisted in time is briefly examined and found to be unsupported.

The Eocene Baltic amber contains a fascinating, although uncommon, bee fauna. Those few specimens that are known present the picture of an assemblage of groups unlike anything seen today. Of the species represented in the Baltic amber only one is currently assigned to a modern genus, this being *Andrena wrisleyi* Salt (1931), although the generic assignment of this species is of considerable question and it is possibly a melittid (Michener and Poinar 1996). The remainder, however, are assigned to extinct genera whose affinities are difficult to ascertain and in some cases cannot confidently be placed to tribe. By comparison, bees of the Dominican amber, which is Oligo-Miocene in age (Grimaldi 1995), are referable to modern day genera or extinct groups closely allied to extant genera (Engel 1995, 1996, 1997, Michener and Poinar 1996, Rozen 1996).

In 1909 Prof. Theodore D.A. Cockerell described a number of Baltic amber Hymenoptera among which was the genus *Electrapis* (1909a). The genus is a member of the corbiculate apine tribe Apini which contains only one other genus, the familiar honey bees (*Apis* L.). *Electrapis* was erected to accommodate the type species *Apis meliponoides* Buttel-Reepen (1906) which, as the specific epithet suggests, possessed characters both Buttel-Reepen and Cockerell took to be intermediate between the Apini and their sister tribe, the Meliponini (the stingless bees). Since the time of its description, *Electrapis* has acquired a total of nine species segregated into three subgenera. Table 1 summarizes the current classification of the known species.

Herein I describe a tenth species of *Electrapis* and assign it to a new subgenus, *Melikertes*. In the descriptions the following abbreviations are used for morphological terms: F, flagellomere; S, sternum; T, tergum. All measurements were made using an ocular micrometer on a WILD-M5a microscope and are in millimeters. All measures are approximate since the best position for viewing a specific structure was not always achievable owing to the curvature of the amber surface. Measurements which were not possible to make for a given specimen are indicated by an asterisk (*). Values given in the specific description are for the holotype with the corresponding measure of the paratype indicated in brackets.

Table 1. Current classification of *Electrapis* species. *Electrapis proava* (Menge) is tentatively included in the subgenus *Melikertes*.

Subgenus	Species	Reference
Electrapis s.str.	*meliponoides*	Buttel-Reepen 1906
Electrapis s.str.	*tornquisti*	Cockerell 1909b
Electrapis s.str.	*apoides*	Manning 1960
Electrapis s.str.	*minuta*	Kelner-Pillault 1970
Electrapis s.str.	*bombusoides*	Kelner-Pillault 1974
Protobombus	*indecisus*	Cockerell 1909a
Protobombus	*tristellus*	Cockerell 1909a
Roussyana	*palmnickenensis*	Roussy 1937
Melikertes	*stilbonota*	present study
?	*proava*	Menge 1856

Genus *Electrapis* Cockerell *Melikertes* Engel, new subgenus

Diagnosis.—*Roussyana*-like species without dense pubescence covering the scutellum; hairs generally sparse, never obscuring integument. Clypeus flat. Labrum U-shaped, broader than long, with apical fringe of simple hairs, hairs laterally short, becoming longer by middle. Labial palpus four segmented, basal segment longest, almost as long as following three segments combined. Minute flabellum at apex of glossa. Antennae set well below mid-line of face; scape slightly curved outwards at apex, inner concave surface without pubescence; pedicel longer than F1; F1 as long as F2 and F3 combined. Compound eyes bare. Face relatively flat. Vertex scarcely elevated above ocelli; preoccipital ridge with a weak carina behind vertex, becoming rounded by gena (Fig. 3). Mesoscutal anterior border weakly rounded, nearly straight; median line and notauli not apparent, parapsidal lines faintly evident. Tegula tear-drop shaped, with blunt apex pointing posteriorly. Scutellum not bulging, surface flat, not reaching back to obscure portions of the metanotum; anterior border nearly straight medially, posterior border broadly rounded. Strigular concavity set on a slightly protuberant shelf; velum and malus simple, velum not divided. Mesocoxae separated medially. Hind tibia without inner apical spurs; corbicula comprising apical three-quarters of hind tibia, posterior apical border rounded; corbicular surface glabrous and not strongly depressed, with a few sparsely scattered long simple hairs, otherwise hairs restricted to tibial lateral borders, such hairs long and branched; inner surface of tibia with a dense medial field of extremely short, simple hairs; strong rastellum on inner apical surface of hind tibia, extending the full width of tibial apex; penicillum absent; hind basitarsus roughly quadrangular, about as broad at base as at apex; attachment to tarsomere 2 set forth on short distal process on anterior border; auricle present; inner surface of hind basitarsus with series of stiff setal rows (as in *Apis*); claw with minute tooth on lower third of inner margin. Pterostigma small; distal wing venation strong; posterior border of second submarginal cell extended posteriorly (Fig. 4), greatly narrowed anteriorly; basal vein basad cu-a, vein relatively straight; cu-a curved outwards, not orthogonal with Cu or A; less than 10 hamuli on anterior margin of hind wing; jugal lobe present, just over one half length of vannal lobe; jugal and vannal incisions shallow. Metasoma without distal rows of hair on terga (Fig. 3).

Type species.—*Electrapis* (*Melikertes*) *stilbonota* Engel, new species, present designation.

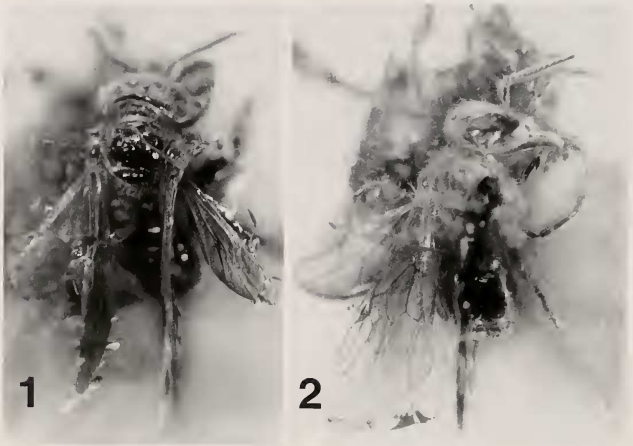
Etymology.—The subgeneric name is taken from the mythology of ancient Crete. Melikertes (meaning "honey-cutter") was associated with Corinth and Melissa, priestess to the mother-goddess Demeter.

Remarks.—*Electrapis proava* is possibly misplaced in *Roussyana* and should be included in *Melikertes*. Official transfer of this species will have to wait, however, until *E. proava* can be studied in more detail.

Electrapis (*Melikertes*) *stilbonota* Engel, new species

(Figs. 1–5)

Description.—FEMALE (male unknown): Body form *Trigona*-like. Total



Figs. 1–2. *Electrapis* (*Melikertes*) *stilbonota* new species. 1, holotype, dorsal view. 2, paratype, lateral view.

body length 3.76 [3.72]. Head wider than long (length 1.10 [1.12], width * [1.32]). Inner margins of compound eyes straight, nearly parallel; upper interorbital distance 0.84 [0.86]; lower interorbital distance * [0.82]; eye length 0.74 [0.76], width 0.32 [0.30]. Gena width 0.28 [0.24]. Mandible with two blunt denticles on upper half of apical margin, length 0.50 [0.44]; malar space length 0.04 [0.06]. Labrum length (median) 0.20 [0.24], width (basal) 0.44 [0.44]; clypeus length * [0.18], width * [0.64]; clypeoantennal distance 0.08 [0.08]. Scape length 0.36 [0.36]; pedicel length 0.10 [0.06]; flagellum length 0.88 [0.86]; F1 length 0.10 [0.10]; F2 length 0.04 [0.04]; F3 length 0.04 [0.04]; F10 length 0.18 [0.18]; F6–10 with dense sensillar plates on inner surfaces; interantennal distance * [0.20]; antennal-ocellar distance 0.58 [0.56]. Median ocellus diameter 0.12 [0.12]; distance between lateral ocelli 0.26 [0.26]; distance between median ocellus and lateral ocellus 0.08 [0.08]; distance from lateral ocellus to eye 0.28 [0.28]; distance from lateral ocellus to occiput 0.16 [0.16]. Mesosoma length 1.34 [1.32]; intertegular distance 0.82 [0.80]; mesoscutum length 0.64 [0.60]; scutellum length 0.26 [0.28], width 0.48 [0.44]; metanotum length 0.04 [0.04]; propodeal triangle over four times longer than metanotum, length 0.18 [0.18]. Mesocoxae separated by more than mesocoxal width; hind tibia length (median) 1.02 [1.02], width (basal) 0.12 [0.12], width (apical) 0.28 [0.30]; hind basitarsus length 0.36 [0.32], width 0.28 [0.28]. Wings hyaline, all veins brown and strong; basal vein basad cu-a by 2 times vein width; pterostigma small; 1m-cu bisecting second submarginal cell; 2r-m distad 2m-cu by 1.5 times vein width; marginal cell length 0.84 [0.86], width 0.24 [0.22]; first submarginal cell shorter than second and third combined; length of anterior border of second submarginal cell one-tenth that of posterior

border; length of anterior border of third submarginal cell half of that of posterior border, just over 3 times length of anterior border of second submarginal cell; forewing length 3.00 [3.16]; venation of forewing depicted in figure 4; six distal hamuli on outer margin of hind wing; cu-a of hind wing orthogonal to M+Cu; hind wing length 2.08 [2.16]; venation of hind wing depicted in figure 5. Metasoma length 1.32 [1.28].

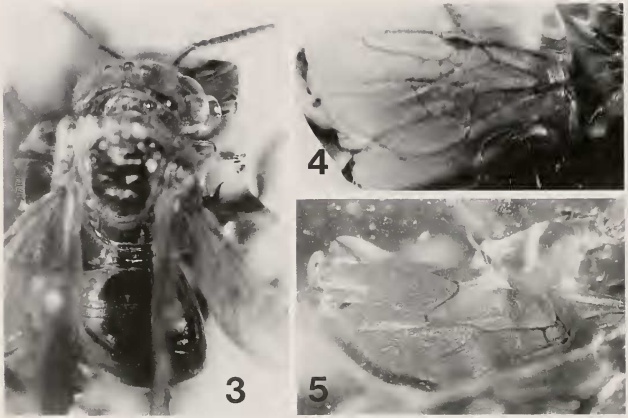
Integument over entire bee smooth and glabrous, except on metanotum where the integument is apparently rugulose. S3–6 apparently weakly nodulate, nodules scattered over the surface, integument between nodules smooth and shining as on previous sterna. Color not well preserved, apparently dark brown to black, metallic and shining, without any maculations.

Pubescence generally pale. Hairs of face widely scattered, simple, and short. Such hairs becoming longer by vertex. Gena with simple, short, suberect hairs. Postgena with long, simple hairs sparsely scattered over integument. Pronotal collar without pubescence; pronotal border with mesoscutum with short, simple hairs; lateral surface with similar minute hairs, such hairs appressed to surface, not obscuring integument. Mesoscutum with scattered simple hairs, more sparsely scattered and shorter over central disc, those hairs on anterolateral borders with a few short branches. Scutellum like that of mesoscutum except pubescence longer and restricted to posterior border. Metanotum with dense, minute, simple hairs, not obscuring the surface. Hypoepimeron without pubescence; mesepisternum with scattered simple hairs, becoming longer ventrally, central disc, however, without hairs. Propodeal triangle and posterior surface without pubescence; lateral surface with scattered long simple hairs and shorter, appressed hairs, partially obscuring the surface. Pubescence of fore- and midlegs generally simple and scattered, except inner surfaces of midtrochanter and femur without pubescence, and outer surface of midtibia with dense, branched hairs. Inner surface of hind femur and trochanter without pubescence, except apical quarter of femur with dense field of minute hairs similar to those on inner surface of hind tibia (see generic diagnosis). Eight comb rows on inner surface of hind basitarsus; outer surface with scattered, long, simple hairs. T1 without hairs over central disc, a few simple hairs on lateral borders. T2 as on T1, except a few simple hairs on posterolateral borders. T3 with simple hairs, longer than those of T1–2, sparsely scattered over central disc, more concentrated on lateral margins. T4–6 similar to T3. Sterna with sparsely scattered simple hairs.

Material examined.—Holotype: female (Figs. 1 & 3), worker, Samland, Eocene Baltic amber, specimen In. 17778, Department of Palaeontology, the Natural History Museum (British Museum, London). Paratype: female (Figs. 2, 4–5), worker, same piece of amber and same accession information as holotype.

Preservation.—The bees presented herein are exceptionally well preserved. The only hindrance to their examination is the uneven surface of the amber and the small block of storage media they are preserved in. A few small fracture planes arising from the wings do not obscure any important structures, although one small fracture near the face of the holotype specimen obscures some features of the clypeus and lower face. A bit of mold on the legs along with the remains of what might have been collected pollen in the corbicula, while slightly demoting them from perfect specimens, does not detract in any significant way from examining their morphology. The inner teeth of the claws are minute and difficult to see. The best view of these structures can be achieved by back-lighting the specimens and examining the extended hind legs.

Etymology.—The specific epithet is derived from *stilbo* (Gr. shine) and *noton* (Gr. back), and is a reference to the glabrous



Figs. 3–5. *Electrapis* (*Melikertes*) *stilbonota* new species. 3, close-up of holotype, dorsal view, showing integument of metasoma and propodeal triangle as well as vertex and preoccipital ridge. 4, left forewing of paratype. 5, left hind wing of paratype.

integument of the dorsum, in particular that of the propodeal triangle.

DISCUSSION

Bees of the tribes Apini and Meliponini are all advanced eusocial, except for a few parasitic forms among the stingless bees (Michener 1974), and, based on their sister-group relationship (Chavarría and Carpenter 1994), presumably inherited this aspect of their biology from a common ancestor that was similarly eusocial. The phylogenetic position of the genus *Electrapis* within the tribe Apini suggests that species of *Electrapis* were also highly eusocial with a well developed caste system. Also suggestive of eusociality among *Electrapis* species is the fact that the specimens described herein are morphologically workers. As in many eusocial species the loss of ovarian development in the worker caste results in a greatly reduced metasoma, a feature seen in both specimens. Similar lines of evidence were used to make the inference that the oldest known fossil bee, *Trigona prisca,* was a worker of a similarly advanced eusocial society (Michener and Grimaldi 1988a, b).

While *Electrapis* runs to the tribe Apini in Michener's (1990) key to the corbiculate bee tribes (treated as subfamilies of Apidae in that work), there are significant enough differences between *Electrapis* and its sister *Apis* which would more than justify placing *Electrapis* in a tribe of its own. Recognition of a separate tribe for these bees, however, would obscure the relationship of *Electrapis* with members of the Apini as both possess a jugal lobe, bifid claws, complete distal wing venation, and a marginal cell apex gently pulled away from the anterior wing margin. A more practical approach to the problem is the recognition of subtribes, retaining a broadly defined Apini. The separation of

Table 2. Brief summary of the subtribal classification of Apini Latreille (based on worker caste). An elaboration of each character is given in the text.

	Apina	Electrapina
Eye hairs:	present	absent
Labral apex:	concave	convex
Mandible:	without dentition	with or without dentition
Vertex:	short	long
Scutellum:	bulging	weakly convex or flat
Propodeum:	short, declivious	long, not declivious
Mesocoxae:	nearly meeting	well separated
Marginal cell:	reaching wing apex	not reaching wing apex
Marginal cell:	not tapering	gently tapering
Basal vein:	distad cu-a	basad to just distad cu-a

these subgroups is as follows (a summary of the differences is given in Table 2):

Electrapina (new subtribe containing only the typical genus *Electrapis*): Compound eyes without hairs; labral apex convex; mandible with or without dentition; malar space extremely short, much less than basal width of mandible; vertex as long as ocellar diameter, or more; scutellum not bulging, surface weakly convex to flat; propodeal triangle with defined surface, not declivious; mesocoxae separated by at least their width; marginal cell not reaching to wing apex, gently tapering over its length; basal vein basad to just distad cu-a, never strongly distad (7 times vein width or more).

Apina: Compound eyes covered with long hairs; labral apex gently concave; mandible lacking dentition; malar space as long as, or longer than basal width of mandible; vertex extremely short, much less than ocellar diameter; scutellum strongly convex and bulging, obscuring metanotum and propodeal triangle; propodeal triangle extremely short and declivious; mesocoxae nearly meeting medially; marginal cell long, nearly reaching wing apex, not gently tapering over its length; basal vein confluent (in some fossil *Apis*) to strongly distad cu-a (over 7 times vein width), never basad cu-a.

Arillo *et al.* (1996) have recently suggested that *Apis* and *Electrapis* overlapped in geologic time. Specimens of *Electrapis* are only known from the Baltic amber which is Eocene in age (Kosmowska-Ceranowicz 1987, Kosmowska-Ceranowicz and Müller 1985) while *Apis* species are unknown until the middle Oligocene (Culliney 1983, Engel in press, Michener 1990, Ruttner 1988, Zeuner and Manning 1976). Thus, the little available evidence in no way suggests that these taxa were coincident in time. Arillo *et al.* (1996) are correct, however, in their assertion that there is no reason to believe *Electrapis* is the direct ancestor of the true honey bees, *Apis*, as has been done by some earlier authors (e.g., Statz 1931, Zeuner and Manning 1976). Lastly, these authors have peculiarly used invalid family-group names for bees. For example, they refer to Michener (1986) for the recognition of Rophitidae in place of Halictidae. In fact, Michener (1986) clearly advises the use of Halictidae (even in his fairly short abstract), a proposal which was later supported by Michener (1991) and validated by the International Commission on Zoological Nomenclature (1993). Therefore, these authors should not be followed in their use of family-group names for bees.

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NOTE ADDED IN PROOF

A paper has recently reached me concerning a Middle-Eocene bee from Germany which is attributable to *Electrapis* [H. Lutz. 1993. *Eckfeldapis electrapoides* nov. gen. n. sp., eine "Honigbiene" aus dem Mittle-Eozän des "Eckfelder Maares" bei Manderscheid/Eifel, Deutschland (Hymenoptera: Apidae, Apinae). *Mainzer naturwissenschaftliches Archiv* 31:177–199]. This bee is clearly a species of *Electrapis* s. str. and, based on the wing venation, appears most similar to *E. apoides*. I, therefore, here synonymize *Eckfeldapis* **(new synonymy)** with *Electrapis*, and place its only included species as a species of the latter: *Electrapis* (*Electrapis*) *electrapoides* (Lutz), **new combination**. It must also be noted that Lutz's figure 3h, labeled as the wing venation of *Apis mellifera*, should be disregarded as it resembles very little the venation of this species (particularly in the position of the basal vein and cu-a).